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ORIGINAL PAPER

Dead wood in clearcuts of semi-natural forests in Estonia: site-type variation, degradation, and the influences of tree retention and slash harvest

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Abstract Semi-natural forests, which naturally regenerate after timber harvesting, provide distinct opportunities for dead wood (DW) management for biodiversity. We described DW pool and sources of its variation during the first decade after final felling in Estonia, hemiboreal Europe. Depending on forest type, the mean post-harvest volumes of above-ground DW ranged from 70 to 119 m^3 ha^{-1}. Final felling generally did not reduce downed coarse woody debris (CWD) because many sawn logs were left on-site, and soil scarification was rarely used. However, subsequent decay of downed CWD appears to be accelerated due to the increased ground contact of logs, so that even the relatively small inputs from live retention trees observed (5 m^3 ha^{-1} per decade) can be ecologically significant. While final felling greatly reduced snag abundance, the mortality of retained live trees generally balanced their later losses. The volumes of downed fine woody debris in conventional cutover sites were roughly double that of pre-harvest forests. Slash harvest caused an approximately twofold reduction in downed DW and resulted in CWD volumes that were below mature-forest levels. The results indicate that the habitat quality of cutovers critically depends both on the retention and on the post-harvest management of biological legacies. In Estonia, the necessary improvements include more careful retention of snags in final felling, selecting larger retention trees, focusing slash harvest on the fine debris of common tree species, and providing snags of late-successional tree species.

Keywords Biological legacy · Coarse woody debris · Fine woody debris · Forest fuel · Snag · Retention forestry

Abbreviations

CWD	Coarse woody debris
DW	Dead wood
FWD	Fine woody debris
STG	Site-type group

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Introduction

Dead wood (DW) that remains on cutover sites after timber harvesting attracts scientific interest for at least three reasons. First, cutovers represent dominant early-successional habitats in human-modified forest landscapes, particularly where even-aged management is practiced (Esseen et al. 1997; Etheridge et al. 2006). Because natural early-successional habitats contain large amounts of DW (which plays major roles in several ecosystem processes and in sustaining biodiversity; Harmon et al. 1986; Siitonen 2001), the DW pool on modern cutover sites and its long-term and large-scale consequences are important to understand. For forest managers, such studies provide a scientific basis for DW retention strategies (Duvall and Grigal 1999; Tinker and Knight 2000; Zabowski et al. 2000). Secondly, cutover legacies comprise mostly harvest-

created fine woody debris (FWD), small pieces of logs, and cut stumps—a composition different from that in natural early-successional habitats (e.g. Pedlar et al. 2002; Eräjää et al. 2010). The ecological functioning (notably habitat provision) of such DW may also be distinct, but it is much less studied than the processes in naturally developed coarse woody debris (CWD) (Siitonen 2001). Thirdly, the reduced and modified DW pool on cutover sites has further become a major target of biofuel extraction in several countries. The environmental effects of forest biofuel extraction are still insufficiently known but are important to predict given the rapid expansion of the practices (Jonsell 2007; Hesselink 2010; Walmsley and Godbold 2010).

In addition to the post-harvest amounts of different DW types, their long-term dynamics are crucial in determining carbon stocks (Janisch et al. 2005), organic-matter inputs to the forest floor (Harmon et al. 1986) and, thus, nutrient stocks in the soil (Yanai et al. 2003) as well as habitat availability and continuity for DW-dwelling organisms on cutover sites (e.g. Ekbom et al. 2006; Sahlin and Ranius 2009). Various management options exist for affecting those functions but both the specific management techniques and the DW targets have been little studied in the field (see Ranius et al. 2003 and Dahlberg et al. 2011 for modelling approaches). In addition to the direct influence of harvesting versus preserving DW, the options include, for example, retaining live trees for future CWD inputs (Rosenvald et al. 2008; Sahlin and Ranius 2009) and avoiding damage to the existing stock during harvesting operations (Jonsson et al. 2010) or soil scarification (Hautala et al. 2004). Obviously, DW dynamics are also influenced by the tree species composition and exposure (Mattson et al. 1987; Næsset 1999; Janisch et al. 2005), which can be manipulated by silvicultural techniques. Finally, on the landscape scale, the approaches can be varied among cutover sites depending on natural conditions and economic considerations.

Semi-natural forests, where timber harvesting is performed in stands that are composed predominantly of native trees established through natural regeneration, can provide distinct opportunities for DW management for biodiversity (Lõhmus and Kraut 2010). However, no explicit studies on the post-harvest DW pool in such forests have been performed in Europe, and thus, these opportunities and the biodiversity costs of management intensification (including biofuel extraction) are not clear. By default, the cutovers of semi-natural forests are likely to comprise a variety of native tree species at near-natural diversity and over their natural range of growth conditions. The large DW losses related to soil scarification (Hautala et al. 2004) are reduced, and unless harvest rotations are very short; clearcuts contain DW of late-successional tree species in sun-exposed conditions. Such habitat features are favourable for biodiversity (Lõhmus 2011).

In this paper, we describe DW pool and major sources of its variation during the first decade after final felling in Estonia—a European country practicing clearcutting-based management of semi-natural forest. We expect that, in such a system, loss of wildlife habitat is mitigated compared with what has been reported for intensive timber production systems (e.g. Siitonen 2001). In particular, the pre-harvesting volumes of CWD in Estonia (Lõhmus and Kraut 2010) often exceed the levels suggested for sustaining wood-dependent species (50 m^3 ha^{-1}; Hanski and Walsh 2004). Hence, even larger DW amounts could be found on recent cutover sites. On the other hand, because clearcutting interrupts the input of woody debris for many years, it is not known whether a shortage of DW-related microhabitats might emerge later on, or which kind. For example, apparently due to progressive wood decay, assemblages of polypore fungi rapidly become impoverished until about 20 years post-clearcutting in Estonia (Lõhmus 2011). It is unknown which DW habitats affect the timing and extent of such biodiversity losses the most, how these vary along environmental gradients, or how they are influenced by novel management techniques, notably tree retention or slash removal.

We combine three studies to answer the following questions:

(1) How do DW amounts and diversity (in terms of species, size, and decay) vary among cutovers of different site conditions? We distinguish three broad types of forest ranging from dry coniferous to moist-to-wet deciduous-dominated forests. We expect that final felling will homogenise their DW supplies, but re-emerging site-dependent features may provide forest type-specific habitats for DW-dwelling wildlife during the subsequent succession.
(2) How quickly does the post-harvest DW of different size fractions degrade, and how does slash removal for biofuel contribute to that degradation? Given the increased decay rates after final felling (e.g. Wei et al. 1997), FWD could decay most rapidly but its input also starts earlier in the regenerating forest; thus, it is not clear how much slash harvest influences the FWD pool or for how long.
(3) How effective is the recent practice of retaining dead and live trees for addressing the shortage of CWD? We focus on standing dead trees (snags), which are key structures for wildlife and abundant in natural post-disturbance habitats, but they are destroyed in conventional clearcutting systems (Duvall and Grigal 1999; Siitonen 2001). We explore to what extent the elevated mortality rates of live retention trees (Rosenvald et al. 2008) can counteract the decay and falling of the pre-harvest cohort of snags, and how large the inputs of downed DW are.

Methods

Study area

The research was carried out in the south-eastern half of the Estonian mainland (Fig. 1), which belongs to the non-oceanic section of the European hemiboreal zone (Ahti et al. 1968). The average air temperature is 16.5 °C in July and −6.5 °C in February; the annual precipitation is 650–750 mm (Aunap 2007). The topography is mostly of glacial origin: flat and undulating moraine plains as well as glaciolacustrine plains with abundant clayey deposits and extensive post-glacial paludification. With two exceptions, all the cutover sites studied were situated <50 m above sea level.

Estonian forestlands (over 2.2 million ha; 51 % of the country) do not contain intensive plantations, >90 % have been naturally regenerated, and thinning intensity is low. However, because of a long history of clearcutting (dominant technique since the nineteenth century), old stands are rare (2 % exceed 120 years' age; Adermann 2009). Typical cut blocks are small (<5 ha) and have had <10 % of growing stock left as solitary retention trees since the late 1990s (Rosenvald et al. 2008). According to the Forest Act, the minimum tree retention requirements "for biodiversity" are at least 5 m^3 ha^{-1} (live and dead trees not distinguished). Nearly, all our study sites (172 of 174) were managed by the Estonian State Forest Management Centre, which has held a Forest Stewardship Council certificate of sustainable forestry since 2002.

The study sites represented productive forests of five site-type groups (STG; based on Lõhmus 1984), which are combined here into three broad types according to natural dynamics and current structure (Lõhmus and Kraut 2010).

(1) Dry boreal forests (mostly *Vaccinium* type dominated by *Pinus sylvestris*; Fig. 2a, b) on higher fluvioglacial landforms and till mounds with podzols (pH 3.5–5.0) where water rises to the soil surface only sporadically and the top layer is periodically dry. These forests have fire-driven natural disturbance regimes, relatively small amounts of harvesting slash per trunk volume (Padari et al. 2010), and more intensive recent management causing a pronounced shortage of DW at the mature stage (Lõhmus and Kraut 2010).

(2) *Oxalis*-type mixed forests dominated either by *Picea abies* or by *P. sylvestris*, and naturally exhibiting successional replacement of tree species after rare wildfires. *Populus tremula* is a characteristic pioneer species and an important retention tree on cutovers (Rosenvald et al. 2008; Fig. 2c, d). This type includes one natural and one artificial STG: (a) meso-eutrophic forests (mostly) on till mounds or rolling plains with podzols or Stagnic Luvisols (pH 3.2–4.2), where groundwater is deeper than 2 m; (b) artificially drained swamp forests (*Oxalis* type), which represent the second post-drainage generation of natural swamp forests and are developing into meso-eutrophic forests.

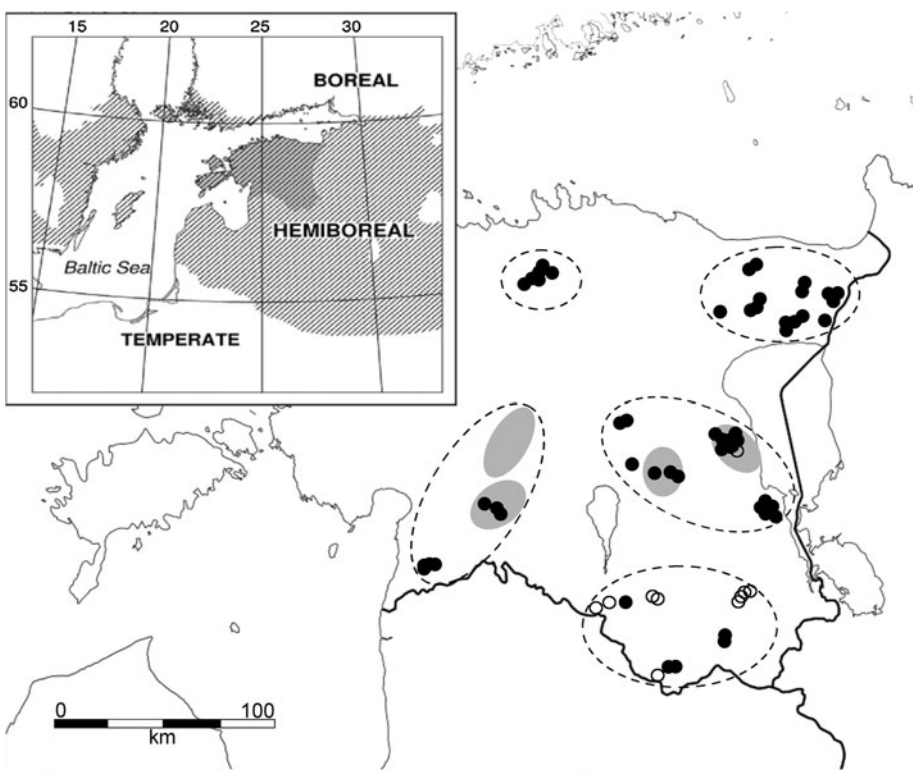

Fig. 1 The study areas in mainland Estonia: cutover sites of study I (*filled symbols*) and study II (*hollow symbols*), and the forest districts considered in study III (*grey ovals*). *Dashed lines* indicate the five regions distinguished in the analyses of downed deadwood (see Table 2)

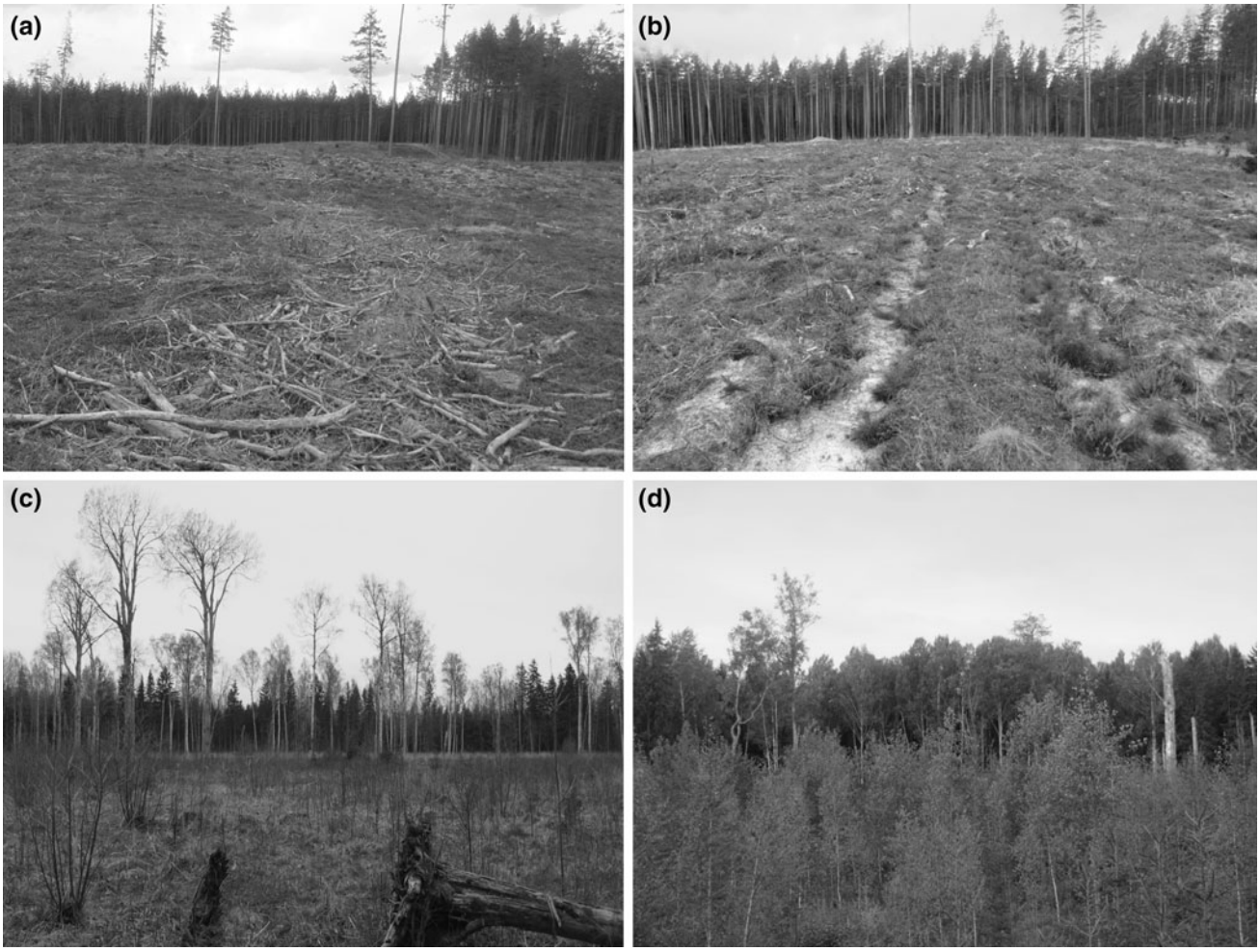

Fig. 2 Examples of the main cutover types included in the study: conventional (**a**) and slash-harvesting (**b**) cutovers of *Vaccinium* type 3 years post-harvest; a cutover of *Aegopodium* type 4 (**c**) and 10 (**d**) years post-harvest (note the heavy loss of retained *P. tremula* trees)

(3) Eutrophic forests, which are usually dominated by deciduous trees (such as *Betula* and *Alnus* species) or *P. abies* and develop naturally through gap-phase dynamics. In terms of STG, these include (a) eutrophic boreo-nemoral forests (mostly *Aegopodium* type) predominantly on undulating sandy till plains with favourably moist (in springtime anaerobic) Gleyic Cambisols or Luvisols (pH 4.7–6.5) and almost no organic horizon; and (b) mobile-water swamp forests on thin flooded Eutric Histosols and Fluvisols (pH 5.0–6.5) in lowlands and valleys along rivers or around bogs.

Study I: variation of dead wood volumes among site types and along succession

Between 2006 and 2009, 58 cutover sites were sampled for a large biodiversity project describing forest management effects in comparison with old forests. A block design of study plots was used to take into account the location (landscape), edaphic conditions (site type), and dominant tree species (see Lõhmus and Kraut 2010). Each of the original 29 blocks represented a cluster of 2-ha plots (different management types of one STG) on a landscape, and each plot represented a different stand. In this paper, we analyse the stand structural data from two types of cutovers (clearcuts without trees retained and retention cuts with solitary retention trees), and we also refer to the published data from mature commercial stands (Lõhmus and Kraut 2010) as an approximation of the pre-harvest situation. There were six clusters (12 cutovers) for each of the five STGs listed above, except the natural swamp forests, for which there were five clusters (10 cutovers). The retention cuts had on average 20 m^3 ha^{-1} of live retention trees (range 2–69 m^3 ha^{-1}), which provided 3 % average canopy cover (maximum 11 %). Soil scarification had only been practiced in four dry forest cutovers.

At the time of the survey, the cutover ages ranged from 2 to 18 years post-harvest (up to 5 years—14 sites; 6–8 years—24 sites; over 8 years—20 sites). The field

methods of measuring DW amounts have been described in detail by Lõhmus and Kraut (2010). In each plot, we used a combination of area-based methods for estimating the densities and volumes of standing trees and the line-intersect method for volumes of downed DW along four straight 50-m transect lines. In structurally poor dry forests, we added 1–2 transect lines in order to increase sample sizes. All the lines were established using a standard map-based procedure prior to fieldwork, with 1–2 lines perpendicular to the main north–south-oriented lines for checking for possible direction-related bias (which was not detected). Thus, for the purposes of this study, one (average) estimate for each plot is used.

We defined CWD as "snags" (standing dead trees ≥1.0 m tall and of diameter at breast height ≥10 cm) and "downed CWD" (including "logs", that is, sawn pieces, as well as naturally fallen CWD ≥10 cm in diameter at the intersection with the line). CWD was sampled all along the lines (snags—within 5 m to both sides of the line, i.e. on 10 % of the plot area). Smaller DW (diameter 0.3–9.9 cm) was classified as FWD and recorded at six 1-m sections established at 10-m intervals on each line (downed items) or on 1 m × 1 m square plots established at those sections (standing FWD; also cut stumps). The diameter, ground contact, and decay stage of downed items were estimated at their intersection with the line. For snags, the measurements were taken at breast height, and the height of snags was also measured. Whenever present, the diameter measurements included bark—because of our comparative aims and focus on biodiversity, we made no attempt to distinguish pure wood volumes. Downed FWD was carefully dissected by hand to detect all intersecting items and their intersection places. We distinguished five decay classes ranging from I (dead for ≤1 year) to V (soft, almost decayed; Lõhmus and Kraut 2010).

Study II: influence of slash harvest

In 2010, the DW pool of twelve cutover sites (2–4 years old; organised as six site pairs) was measured in south-eastern Estonia following the field methods of study I. Each site pair comprised one conventionally harvested and one slash harvest site of the same STG and similar age (Fig. 2a, b).

Three STG on mineral soils were considered (swamp forests are too wet for slash harvesting), and two site pairs (4 cutovers) were sampled per STG. The pre-harvest forests had been dominated by (1) 100- to 120-year-old *P. sylvestris* trees in the dry boreal sites; (2) by 90- to 115-year-old *P. abies* or *P. sylvestris* trees in the meso-eutrophic sites; and (3) by 60- to 85-year-old *Betula pendula* or *P. tremula* trees in the eutrophic sites of the *Aegopodium* type. All the stands had been managed for timber production; their areas ranged from 0.6 to 3 ha (average 1.9 ha) and within-pair distances up to 7 km (average 2.9 km). The final felling (with solitary trees retained) had been performed with a harvester in 2006–2008; slash had been collected directly after that using forwarders. The forwarder operators determined the amount of slash worth being extracted on the site. According to the Estonian FSC standard (Oja 2009), the amount of downed DW to be left should resemble that present in the pre-harvest stand (≥10 m^3 ha^{-1} of downed CWD ≥20 cm in diameter). Soil scarification had been practiced in one conventional and in two slash-harvested cutovers.

Study III: snag dynamics

This study is based on monitoring a full set of retention cuts from two subsequent years (2001—71 sites; 2002—33 sites) in three Estonian regions (Fig. 1). Details on the design and 6-year results on live retention trees have been published by Rosenvald et al. (2008). The mean area of the cuts was 2.3 ha (range 0.3–6.9 ha). The dominant STGs, according to pre-harvest composition, were deciduous-dominated eutrophic boreo-nemoral (58 sites; mainly *Aegopodium* type) or *Pinus* or *Picea*-dominated meso-eutrophic forests (26 sites; mainly the *Oxalis–Vaccinium myrtillus* type). At the time of harvest, the deciduous stands had been mostly 50–80 (max. 110) years old, and the conifer stands had been 90–110 (max. 180) years old.

In March–April 2002, all live trees and snags >1.5 m tall and with a diameter at breast height ≥14 cm were mapped in the field, and their species, diameter, height of snags, and condition were recorded. Every subsequent summer until 2011, each tree was described in terms of its survival, cause of death and type of damage if present (including changes in height), and (in case of snags) the relative cover of exposed wood and bark within 2 m (visually estimated to the nearest 10 %, except for classes 1 and 5 %). The causes of tree death were classified as trunk breakage creating a snag, windthrow (including breakage at <1.5 height), or death standing (cause unknown). In 2010, the relative cover of exposed wood and bark on the whole trunk and decay stage (5 classes; see Study I) was estimated for each snag. In total, there were 760 snags at the beginning of the study and 701 snags at the end (Table 1).

Data processing

The main analyses of studies I–II were focused on downed DW, the volume of which was estimated assuming circular cross-sections (Warren and Olsen 1964; Van Wagner 1968). We omitted the cutover-scale estimates that were based on <3 DW items measured. The initial explicit GLM analyses explaining the volume of four DW fractions in conventionally harvested cutovers (including six such

cutovers of study II) revealed: (1) no difference between retention cuts and clearcuts in any model ($p = 0.24$–0.97); (2) some significant differences between regions (see Table 2); and (3) no significant STG differences within our broad forest types. Based on that screening, we estimated the absolute annual volume reductions using reduced models for each forest type that was only comprised of cutover age and region as a covariate (random factor). Because we lacked cutovers of <2 years' age, we predicted post-harvest volumes (for year = 0) from linear regression comprising the cutover age. We used linear approximations because the samples were too small for establishing non-linearity, and the differences of model predictions would be very small for the 2-year period (particularly when considering initial delays in DW volume loss; Harmon et al. 1986). Since long-term dynamics are hardly linear, our results should not be translated to extended timeframes.

In similar GLM analyses, which incorporated forest type, we also estimated (separately for downed FWD and CWD) the influence of post-harvest time on habitat quality characteristics (Shannon indices of species diversity and decay stage diversity; the proportion of deciduous DW and well-decayed wood; the proportion buried under slash or in litter or moss, and above the ground lacking ground contact). All those calculations were based on volumes. The species diversity estimates for FWD are probably conservative because the species of well-decayed deciduous twigs were often difficult to identify. We also combined the data from mature pre-harvest forests for comparison with the post-harvest volumes (Table 2).

The reductions in downed DW due to slash harvesting could be only roughly assessed because before-and-after comparisons were unavailable. Although we had paired control (i.e. conventionally harvested) sites, that comparison depends on the local tradition of "cleaning" cutovers, there is no established level of downed DW retention in Estonia. Therefore, we compared the DW volumes in slash harvest cutovers both with those in the control cutovers and with the mean values for the same forest types in Estonia.

The volumes and surface areas of the trunks of live trees and snags were estimated according to species-specific diameter functions (Padari 2004) used in practical silviculture in Estonia. For that, the height of intact standing trees was estimated from the measured diameter and site quality class using an extensive set of model trees all over Estonia (see Sims et al. 2009). The volume of stumps was calculated with the formula of a cylinder.

In study III, we calculated annual volume changes of retained snags (dead at the time of harvest) and new snags (created by the death of live retention trees) based on their mean volumes in the 104 cutover sites; we also estimated the amounts of downed CWD created by falling of the retention trees. Because absolute volumes depend on retention levels, the dynamics were expressed as relative volumes compared with the initial volume (snags) or final volume (downed CWD created by treefall). The data of the 10th post-harvest year only include the cutovers of 2001.

We performed two multifactor logistic regression analyses to identify the main determinants of the decadal persistence of individual retained snags. Persistence (scored 1) was defined as "not fallen" or "standing intact in terms of height" by the 9–10th post-harvest years, respectively. Four variables were considered (STG; tree species; tree diameter; initial height of the snag), of which those not significant in the full type III model were eliminated to reach a final model. We also performed two assessments of the bark and wood microhabitats in snags. For individual new snags, we annually followed their bark cover on the lower 2 m of the trunk. According to the data collected in 2010, those estimates were well correlated with the estimates for whole trunks (depending on tree species, $r = 0.75$–0.92, $p < 0.001$). The whole-trunk data of 2010

Table 1 Post-harvest numbers of live trees and snags by tree species in the cutover sites of study III (in 2001 or 2002; total area 236.4 ha), and their persistence as live trees or snags by 2011 ("new" snags originate from live retention trees)

Tree species	Post-harvest		In 2011				
	Live trees	Snags	Live trees	Snags		Fallen	
				Persisted (%)	New	Live trees	Snags
Betula spp.	1,030	333	506	122 (37)	165	359	211
P. tremula L.	458	106	211	40 (38)	121	126	66
P. sylvestris L.	651	66	347	47 (71)	42	262	19
P. abies (L.) Karst.	47	137	27	61 (45)	3	17	76
F. excelsior L.	577	0	443	0	58	76	0
Alnus spp.	137	108	106	18 (17)	13	18	90
Other	361	10	253	5 (50)	6	102	5
Total	3,261	760	1,893	293 (39)	408	960	467

Table 2 Estimated post-harvest volumes of downed dead wood on cutovers, and its reduction during the subsequent years in dry forests ($n = 14$; time frame 18 years), *Oxalis* type ($n = 26$; time frame 13 years) and eutrophic forests ($n = 24$; time frame 10 years)

DW fraction/forest category	Post-harvest volume[a]		Annual volume change[b]		
	m^3 ha^{-1} (±SE)	%[c]	m^3 ha^{-1} (±SE)	*p*	%
Diameter <1 cm					
Dry forests	4.2 ± 1.4	334	−0.2 ± 0.1*	0.061	−5.2
Oxalis-type forests	6.0 ± 1.0	128	−0.3 ± 0.2	0.080	−5.1
Eutrophic forests	3.3 ± 0.6	109	−0.1 ± 0.1	0.134	−4.2
Diameter 1.0–4.9 cm					
Dry forests	26.5 ± 6.1	514	−1.5 ± 0.8	0.082	−5.7
Oxalis-type forests	33.0 ± 4.0	366	−1.9 ± 0.6	0.003	−5.9
Eutrophic forests	23.4 ± 4.5	210	−0.4 ± 0.7	0.564	−1.8
Diameter 5.0–9.9 cm					
Dry forests	9.8 ± 6.6	123	−0.4 ± 0.5*	0.379	−4.4
Oxalis-type forests	28.5 ± 5.8	348	−2.5 ± 0.7*	0.003	−8.8
Eutrophic forests	11.4 ± 7.8	98	−0.9 ± 1.2	0.460	−8.0
Diameter ≥10 cm					
Dry forests	17.4 ± 7.2	238	−1.5 ± 0.9	0.134	−8.4
Oxalis-type forests	28.2 ± 12.4	77	−1.8 ± 1.6*	0.277	−6.4
Eutrophic forests	47.8 ± 9.4	141	−3.8 ± 1.5	0.020	−7.9

[a] Estimated for year 0 post-harvest across all regions (cf. Fig. 3)

[b] Compared with the mean post-harvest volume: regression slopes and their significance levels in GLMs taking into account the region; the fractions having regionally significantly varying volumes are indicated with asterisks (*)

[c] Compared with mean volumes in mature commercial forests (Lõhmus and Kraut 2010, reanalysed)

were additionally combined with the calculated surface areas of all snags in that year to get cutover-scale areas of snag bark and snag wood microhabitats.

Results

Site variation and post-harvest degradation of DW (studies I–II)

The downed DW pool of conventionally harvested cutovers (no slash extraction) differed clearly between the three forest types. The average estimated total volumes for year 0 after the final felling ranged from 58 m^3 ha^{-1} in dry forests to 86 m^3 ha^{-1} in eutrophic forests and 96 m^3 ha^{-1} in *Oxalis*-type forests, the share of CWD being 30, 56, and 29 %, respectively (Table 2). Final felling caused the largest inputs of the small fractions (<5 cm in diameter) in dry forests (three- to fivefold increases compared with mature-forest levels). Although the volume estimates for that FWD varied widely and its decadal reduction only emerged as marginally significant, the coefficients indicated that its loss was not slower than in other forest types (Table 2). At the other extreme, FWD volumes in the eutrophic forests either did not increase at all or (medium-sized FWD) just doubled with final felling, while the later declines of the two smallest fractions were relatively small and non-significant. However, CWD declined consistently (significantly) over the post-harvest decade only in eutrophic forests (Fig. 3); in the diameter class of 5–9.9 cm, a similarly large DW pool and its consistent decline were observed in the *Oxalis*-type forests (Table 2).

Progressive degradation and increased burial and ground contact were the main decadal changes in downed DW (Table 3). The composition of CWD shifted to a significantly more decayed stage than the FWD within 10 years (Fig. 4); however, the diversity of decay stages had no significant trend. At the time of the surveys, 4.3 % of the total volume of downed CWD was formed by fallen retention trees. There were no significantly changes in species composition or diversity of downed DW (but note a tendency of reduction in the case of species diversity of FWD; Table 3).

Cut stumps were by far the most abundant items of standing DW both in terms of density and volume (Fig. 5). Their availability was smaller in dry forests both because of a lower mean density (659 stumps ha^{-1}) and height (21 cm) compared with that in the other forest types (1,004 stumps ha^{-1} and 29–30 cm height). Thus, the approximate mean above-ground volumes of stumps ranged from 7.9 m^3 ha^{-1} in dry forests to 13.6 m^3 ha^{-1} in eutrophic forests and 19.9 m^3 ha^{-1} in *Oxalis*-type forests.

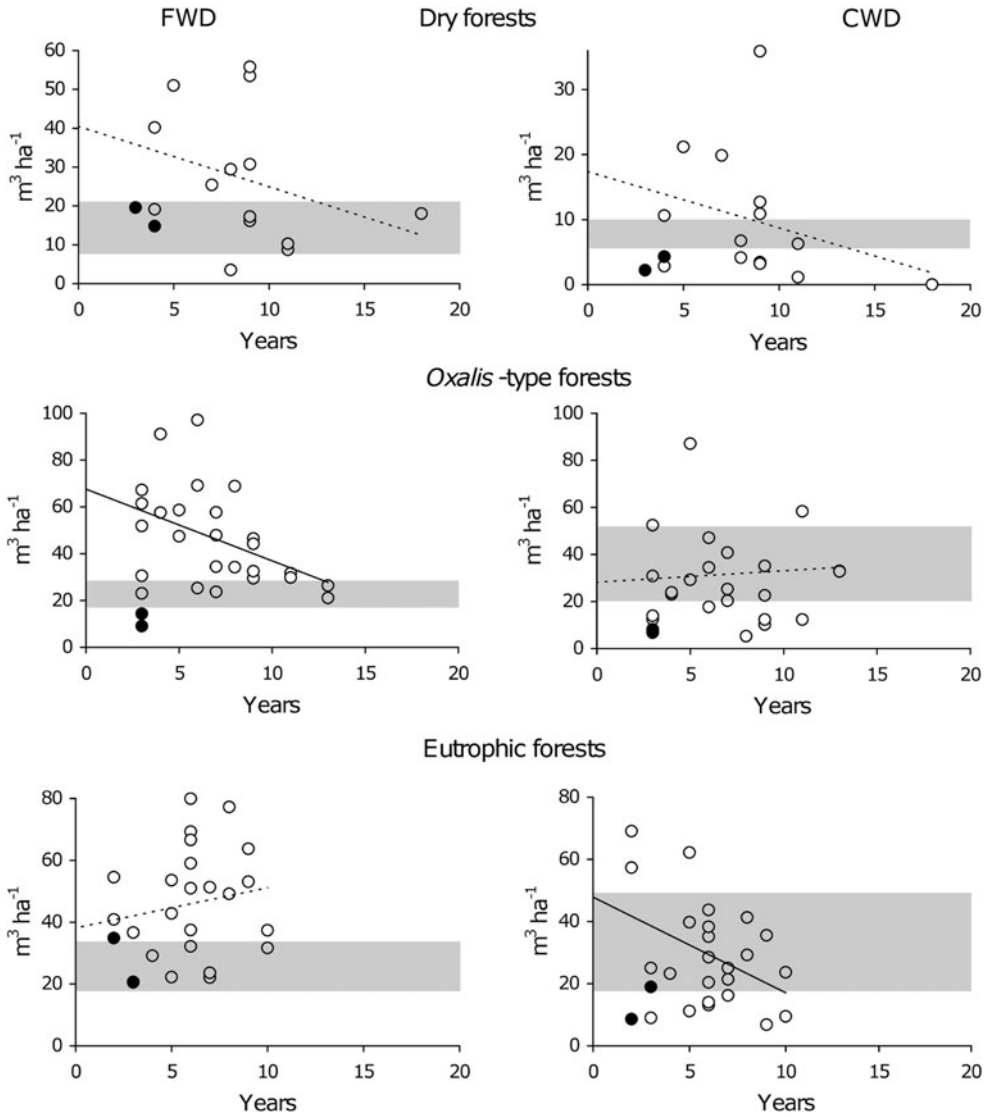

Fig. 3 Volumes of downed FWD (<10 cm in diameter) and CWD by forest type and along cutover age. *Hollow symbols* depict conventional cuts; the regression lines are provided for general illustrative purposes only (*solid lines* significant at $p < 0.05$; *dashed lines* non-significant)—see Table 2 for the slopes in multifactor analyses. *Filled symbols* depict slash-harvesting sites. The *grey area* covers 95 % CI for the mean values in pre-harvest mature stands (modified from Lõhmus and Kraut 2010)

Only 3 % of cut stumps exceeded 0.5 m in height. Snags over 1.5 m tall only formed 0.6 % of standing DW items and 9.6 % of the volume (Fig. 5).

Taken together, the estimated mean volumes of above-ground DW were 70 m^3 ha^{-1} in dry forests, 119 m^3 ha^{-1} in *Oxalis*-type forests, and 103 m^3 ha^{-1} in eutrophic forests.

Influence of slash harvest (study II)

Based on comparisons with conventional cutovers, the influence of slash harvest was pronounced both for downed FWD (particularly in the *Oxalis* type) and for CWD (in every forest type; Table 4). The volumes of CWD in the slash harvest sites (but not in conventional cutovers) tended to be consistently lower than those in mature commercial stands (Fig. 3). However, the share of FWD buried under litter was significantly smaller in the slash harvest sites (mean 24 ± 9 %, SD) than in conventional cutovers (37 ± 6 %; mean pair-wise difference 14 ± 8 %; *t* test for paired samples: $t_5 = -4.4$, $p < 0.001$).

CWD dynamics in relation to tree retention (study III)

The average post-harvest volumes of snags were 1.02 ± 0.39 (95 % CI) m^3 ha^{-1} of deciduous trees and 0.38 ± 0.17 m^3 ha^{-1} of conifers, of which only 36.6 % (0.37 ± 0.22 m^3 ha^{-1}) of deciduous snags and 53.8 % (0.20 ± 0.12 m^3 ha^{-1}) of conifer snags were still standing after the first decade (see also Table 1). The persistence depended primarily on two factors: it increased with tree diameter and varied among tree species (best in *P. sylvestris*, worst in softwood deciduous trees; Table 5). Although the initial snag height also had a marginal negative effect on survival, the actual effect is probably non-linear since intact dead trees and medium-height snags

Table 3 Volume-based characteristics of the downed dead wood pool by site type and cutover age (dry forests pooled due to the small sample size)

Variables	Mean ± SE by forest type and cutover age					Trend p[a]
	Dry forest	*Oxalis*-type forest		Eutrophic forest		
		2–5 year	6–13 year	2–5 year	6–10 year	
n	14[b]	9	17	8	16	
FWD (<10 cm)						
Species diversity[c]	0.5 ± 0.1	1.1 ± 0.1	0.8 ± 0.1	1.1 ± 0.2	1.0 ± 0.1	0.070
Decay stage diversity[c]	0.9 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	0.8 ± 0.1	1.0 ± 0.1	0.311
% Deciduous wood	6 ± 2	41 ± 9	53 ± 6	58 ± 10	59 ± 8	0.336
% Well decayed[d]	26 ± 6	11 ± 2	21 ± 4	9 ± 2	19 ± 3	<0.001
% Buried	41 ± 4	28 ± 6	41 ± 4	26 ± 6	43 ± 4	0.001
CWD (≥10 cm)						
Species diversity[c]	0.2 ± 0.1	0.9 ± 0.1	0.6 ± 0.1	0.8 ± 0.2	0.8 ± 0.1	0.296
Decay stage diversity[c]	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.628
% Deciduous wood	4 ± 3	45 ± 11	53 ± 8	68 ± 12	61 ± 8	0.786
% Well decayed[d]	25 ± 6	14 ± 5	34 ± 5	16 ± 5	26 ± 4	<0.001
% Sawn logs[a]	68 ± 7	70 ± 9	58 ± 7	40 ± 12	48 ± 7	0.794
% Above the ground	4 ± 2	15 ± 5	5 ± 1	16 ± 8	9 ± 3	0.043

[a] Significance of the time since final felling in GLM models also incorporating forest type

[b] In the case of CWD, three cutovers with <3 observations have been omitted

[c] Shannon index values

[d] Decay stages IV–V (according to Lõhmus and Kraut 2010)

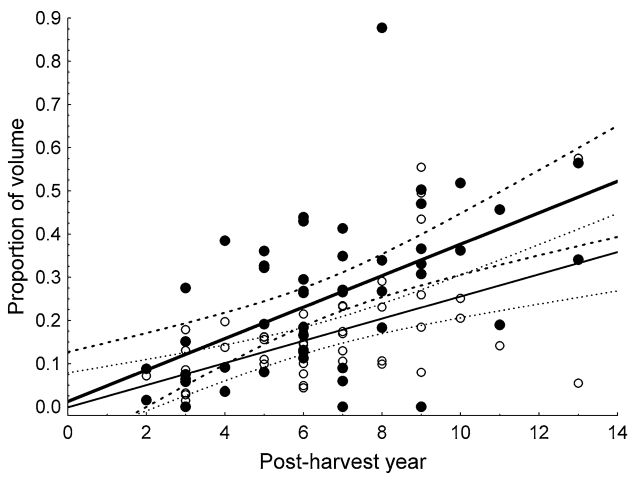

Fig. 4 Proportion of well-decayed (decay stages IV–V) downed FWD (<10 cm in diameter; *hollow symbols* and *thin* regression line) and CWD (*filled symbols*, *thick* regression line) in relation to time since final felling. *Dashed lines* depict 95 % CI for the regression lines

appeared to suffer the most (Online Resource 1). Additionally, taller and thinner snags, particularly of deciduous trees, had a considerably higher probability of trunk breakage (shortening) during the decade (Table 5).

The post-harvest dynamics of CWD were fundamentally influenced by the death of live retention trees, of which over 40 % (both by numbers and by volume) died during the first decade. In deciduous trees, 10.2 % of that total volume became snags and 33.3 % became downed woody debris; in conifers, 3.9 and 41.2 %, respectively. As a result, the final volume of new deciduous snags averaged 1.04 m^3 ha^{-1} and the total snag amounts increased (Fig. 6a), while the decadal input was only 0.15 m^3 ha^{-1} in conifers and their amounts decreased (Fig. 6b). The main cause for the latter was the rapid loss of spruce snags, which were not replaced because live individuals of that species were rarely retained (Table 1). The mean decadal inputs of downed CWD were 3.28 m^3 ha^{-1} of deciduous logs and 1.81 m^3 ha^{-1} of conifer logs. Most of that originated from windthrow or breakage of live retention trees; only 19.7 % (0.65 m^3 ha^{-1}) of deciduous and 9.6 % (0.17 m^3 ha^{-1}) of coniferous downed CWD were created by the fall or breakage of retained snags (Fig. 6c, d). Due to extensive dieback of *Fraxinus excelsior*, the CWD input of that species was large; however, those root-rot damaged trees only stayed standing for a few years after death (the average time was 2.77 years in 35 fallen trees; maximum 7 years in one case).

The dynamics of wood and bark microhabitats on snags were tree species specific. In *P. sylvestris*, the mean cover of exposed wood already exceeded 50 % of trunk surface in the second year after death, and it was almost invariably 100 % by year 10. The development of exposed wood area was slightly slower in *P. tremula* and distinctly slow in

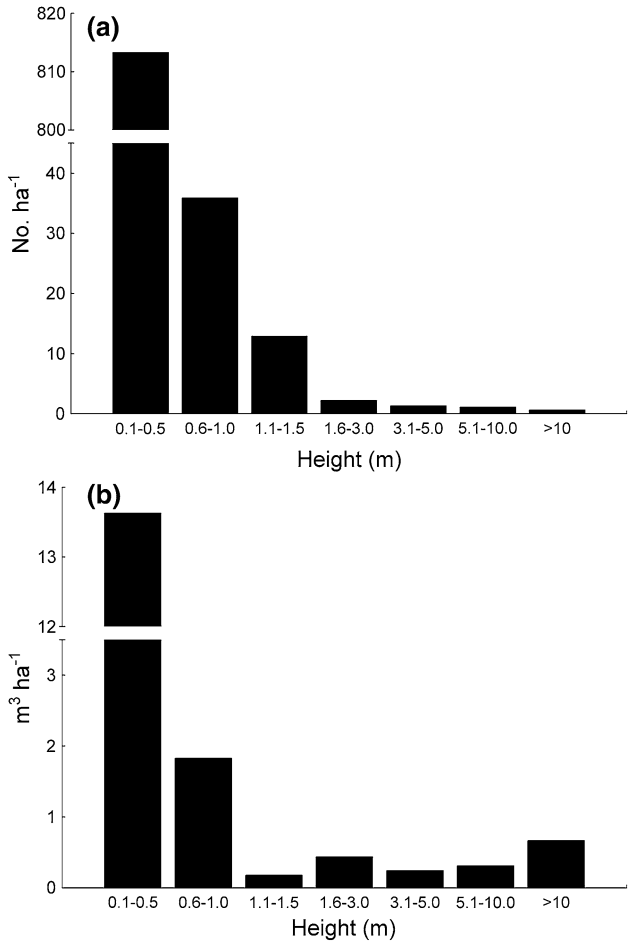

Fig. 5 The average density (**a**) and volume (**b**) of standing dead wood by height class in 64 Estonian cutover sites (studies I–II). The items considered were ≥10 cm in diameter at breast height or, in the case of shorter items, at the top. Note the scale break for the shortest items (cut stumps)

Table 4 Estimated effects of slash harvesting: the average volumes of downed dead wood in two harvested cutovers for each basic forest type when compared with two adjacent "control" cutovers and average expected values for cutovers of that age (see Fig. 3)

Fraction	Forest type	Volume (m^3 ha^{-1})			% Harvested
		Harvested	Control	Expected	
FWD (<10 cm)	Dry	17.2	29.7	35	42–49
	Oxalis	11.7	26.8	59	56–80
	Eutrophic	27.7	37.6	41	26–32
CWD (≥10 cm)	Dry	3.2	6.7	14	52–77
	Oxalis	7.6	9.6	30	20–75
	Eutrophic	13.8	47.1	41	66–71

Betula spp. where it only reached 36 % in 10 years (Fig. 7).

On the cutover scale, the mean total surface area of snags comprised 13 m^2 ha^{-1} of exposed wood and 10 m^2 ha^{-1} of bark cover at the end of the first decade (Table 6 in Online Resource 2). That exposed wood was mostly (86 % of area) in decay class II (weakly decayed) and, within this decay class, 42 % was formed by large *P. tremula* snags and 30 % by *P. sylvestris* snags. Half of exposed wood area originated from originally retained snags, which represented various tree species and sizes. Among new snags, 56 % of total wood surface was made up by large *P. tremula* individuals. Bark-covered snag area also mostly (70 %) belonged to decay class II (Table 6) but that weakly decayed surface also comprised, in addition to large *P. tremula* snags (23 %), many *Betula* spp. (31 %) and newly dead, usually small *F. excelsior* trees (30 %). Most bark-covered snags of advanced decay (by area: 83 % of decay class III and 90 % of decay class IV) or >5 years since death were of *Betula* spp., which represented both retained and newly developed snags (Table 6).

Discussion

Influence of final felling on dead wood pool

Our study supports the view that conventional clearcuts in semi-natural forests have a considerably richer DW pool, with distinct post-harvest dynamics, compared with clearcuts in intensive plantation-based forestry. This resulted not only from a richer DW pool in pre-harvest forests (Lõhmus and Kraut 2010), but also from the weaker effects of final felling (see also McCarthy and Bailey 1994 for a North American study). In addition to the habitat provisioning function, DW obviously formed the main aboveground storage of organic matter and nutrients throughout the first post-harvest decade in these semi-natural forests.

In particular, downed CWD *volumes* generally did not decline in final felling in Estonia (Fig. 3), while approximately threefold reductions are reported in the intensively managed forests of neighbouring hemiboreal Sweden (Fridman and Walheim 2000). Clearly, a significant part of CWD reduction attributed to final felling is instead caused by the subsequent soil scarification (Hautala et al. 2004) or, in some other management systems, by slash burning (Benson 1982). However, final felling apparently destroyed a large proportion of downed DW *items* of the pre-harvest forest—given that about half of the "retained" CWD volume consisted of sawn logs, and there was significant input from damaged snags (see below). Such an abundant legacy of sawn logs, in combination with the regional differences in DW volumes (note that these were characteristic of the best accessible forest types; Table 2), also highlights the importance of the social and economic context for DW management. Thus, in Estonia, the initial post-harvest DW pool apparently depends on local traditions and

Table 5 Multifactor logistic regression models for the decadal persistence of snags (general persistence as a snag, and persistence of initial height in snags that survived)

	Persistence of snag (LL model = −469.9, $p < 0.001$, $n = 760$)				Persistence of initial height (LL model = −129.8, $p < 0.001$, $n = 360$)			
	Estimate ± SE	LL	Stat.[a]	p	Estimate ± SE	LL	Stat.[a]	p
Intercept	−1.06 ± 0.25		18.5	<0.001	3.40 ± 0.75		20.9	<0.001
Initial height, m	−0.03 ± 0.01	−472.6	5.5	0.019	−0.39 ± 0.06	−183.8	108.0	<0.001
Diameter, cm	0.04 ± 0.01	−479.4	19.0	<0.001	0.07 ± 0.02	−135.9	12.2	<0.001
Tree species		−498.0	56.1	<0.001		−228.7	197.6	<0.001
Pinus	1.45 ± 0.24		37.4	<0.001	5.70 ± 1.03		30.6	<0.001
Picea	0.09 ± 0.17		0.3	0.592	2.14 ± 0.65		10.9	<0.001
Populus	−0.29 ± 0.19		2.4	0.123	−1.45 ± 0.51		8.1	0.004
Betula	−0.20 ± 0.13		2.4	0.120	−3.55 ± 0.46		58.7	<0.001
Other[b]	−1.04 ± 0.21		25.0	<0.001	−2.85 ± 0.56		25.7	<0.001

LL log-likelihood

[a] χ^2_1 of likelihood ratio tests for the main variables (in bold); Wald statistic for the differences between tree species

[b] Softwood deciduous trees, such as *Alnus* spp. and *Salix caprea*

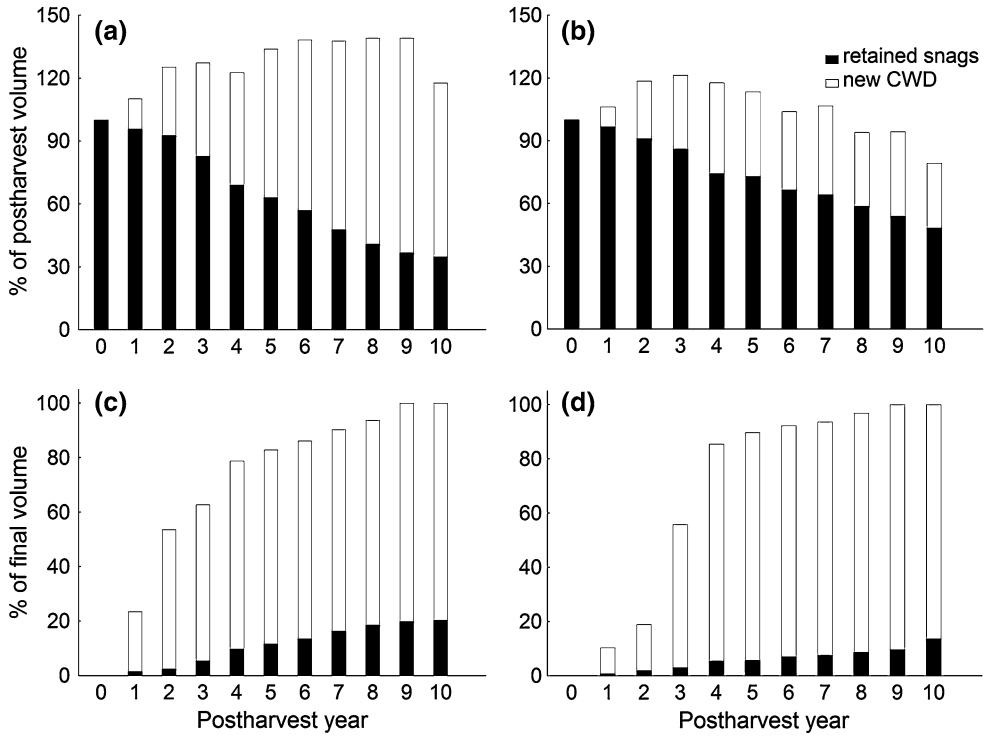

Fig. 6 Development of relative post-harvest volumes of deciduous (**a**) and conifer snags (**b**), and of downed woody material that originates from the fall of retained deciduous (**c**) and coniferous (**d**) trees. Reference years are at post-harvest (**a**, **b**) or year 9 post-harvest (**c**, **d**); originally retained snags and the inputs from retained live trees (new CWD) are distinguished

considerations of (not) "cleaning" cutover sites, the effects of which may, in the case of slowly decaying CWD, last for decades after stand initiation (Lõhmus et al. 2005).

The only major reduction caused by final felling was observed for snags, which, however, is mostly avoidable (e.g. Jonsson et al. 2010) and should be addressed by managers in the future. In our two data sets (differing in size criteria for inclusion), snags formed 1–2 m^3 ha^{-1} in cutover sites, while their pre-harvest levels in Estonian mixed and deciduous forests are 12–15 m^3 ha^{-1} (Lõhmus and Kraut 2010). Compared with natural post-disturbance forests, the reductions are obviously much larger (e.g. Duvall and Grigal 1999). Although broken snags were apparently added to downed CWD pool, such transformation cannot compensate for ecological functions lost. For example, the scarcity of snags is a major factor explaining the low species richness of calicioid fungi—a taxon group with many wood-inhabiting species—in cutover sites

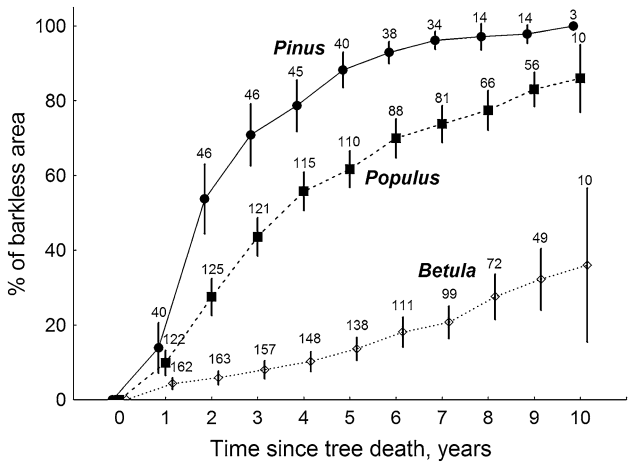

Fig. 7 Mean relative cover of exposed wood (±95 % CI) on snags up to 2 m height in relation to their time of death on cutover sites. Only the snags created by the death of live retention trees are shown; the *numbers* denote sample sizes

(Lõhmus and Lõhmus 2011). In forests that burn (such as the dry boreal type), snag abundance is the main factor accounting for distinct bird assemblages in natural early-successional areas (Hobson and Schieck 1999). Cut stumps and short snags, which were abundant on cutovers, can perhaps sustain some snag-inhabiting cryptogams and insects of conservation concern, but this requires explicit study (e.g. Caruso and Rudolphi 2009).

Influence of slash harvesting

Volumes of downed FWD (the main target of slash harvest) were roughly twice as large in cutover sites as in Estonian pre-harvest forests (Lõhmus and Kraut 2010). The exceptionally low volumes of the <1 cm fraction in eutrophic forests (Table 2; similar to pre-harvest levels) may reveal heavier destruction by the harvest machinery of the deciduous twigs dominant in such forests. The FWD volumes reported for conventional clearcuts in the intensively managed Nordic forests vary from <2 m^3 ha^{-1} (Caruso et al. 2008) to 10 m^3 ha^{-1} (Eräjää et al. 2010), which (omitting the finest fractions that were not measured in those studies) are roughly 3–6 times smaller than those found by us. The effect of intensive forestry per se is probably smaller, because Estonia naturally has higher FWD volumes (Lõhmus and Kraut 2010), and our field methods included buried FWD and no minimum lengths for the items considered. Nonetheless, it is likely that, similarly to CWD, the FWD amounts in semi-natural cutovers exceed those left by the Nordic forestry practices. This is because both size fractions are affected by the same main processes of DW reduction (see above). Indeed, the share of FWD in the whole pool (ranging from one-third in eutrophic cutovers to about half elsewhere) was similar in our study and, for example, that reported by Eräjää et al. (2010) for central Finnish spruce stands.

One might conclude that the approximately twofold reduction in the FWD pool caused by slash harvest does not have significant ecological impacts (and note that microhabitats for epiphytic and epixylic species suffered even less due to the increased relative exposure of FWD items). However, three observations raise conservation concern. First, the Estonian practice included much larger simultaneous removals of CWD than in the Nordic countries (Rudolphi and Gustafsson 2005; Eräjää et al. 2010). Thus, it represented a general step towards management intensification rather than targeted harvesting of slash. Secondly, FWD removals were highly forest type dependent, apparently reaching the highest levels in *Oxalis*-type stands (Table 4). Although we acknowledge our limited samples, a precautionary view is that the DW pool in such spruce-dominated forests is most vulnerable to impoverishment: already following slash harvest, FWD and CWD supplies were both below the pre-harvest mature-forest levels there (Fig. 3), but these forests are also the most convenient targets of future stump harvesting. Thirdly, the importance of the FWD pool in cutovers is largely related to its species diversity (Table 3), that is, the wood of some tree species is often present as FWD only. Hence, in species-rich stands with dense undergrowth and/or rare woody plants present, even moderate FWD reductions may eliminate substrates for some specialised wood-inhabiting species (see also Jonsell et al. 2007). To summarise, there is a general necessity to increase selectivity of slash harvest techniques (Dahlberg et al. 2011), considering the specificity of semi-natural forests in terms of wood fractions, species diversity, and forest types.

Dead wood provision from live retention trees

Recent research has documented significant inputs of CWD from live retention trees due to their increased mortality in the open conditions of cutovers (Jönsson et al. 2007; Rosenvald et al. 2008; Sahlin and Ranius 2009). We demonstrated that this input could provide a relatively stable stock of diverse bark and exposed wood microhabitats of different tree species, which is a desired outcome from tree retention. Obviously, the main prerequisite for that, and a major advantage of semi-natural forests, is the species diversity of mature commercial forests.

For the general stability of snag amounts, the proportion of roughly 80 % live trees and 20 % snags among retained stock appeared to work well (Table 1). Large reductions in the first years (Smith et al. 2009) were avoided, although signs of a later (expectable) decrease appeared by the end of the first post-harvest decade (Fig. 3a, b). That decrease results both from a limited input of new snags (reduced

live-tree stock and its reduced mortality; Rosenvald et al. 2008) and loss of existing snags. Our analysis indicated that snag persistence can be improved by retaining larger trees, which are also more likely to host specialised biota (e.g. Sahlin and Ranius 2009). Since larger live individuals of most deciduous trees (except *Betula* spp.) survive better on retention cuts (Rosenvald et al. 2008), that may expand the period of snag inputs (at the expense of the initial increase) and further stabilise their dynamics. Thus, selecting larger retention trees is probably a more cost-effective strategy than increasing the number of trees retained. However, the pre-harvest size of trees is ultimately limited by rotation length in even-aged management systems.

The main biodiversity-related problem with the post-harvest snag availability in Estonia was the lack of particular tree species: a rapid loss of spruce snags and small numbers of retained snags of "noble" hardwoods (*Acer platanoides*, *F. excelsior*, *Quercus robur*, *Ulmus* spp.). Live spruces are avoided as retention trees because of their susceptibility to uprooting; the prevalence of uprooting also inhibits the formation of snags of *Tilia cordata* (Rosenvald et al. 2008). The late-successional hardwoods are generally rare and/or mostly stay in the understory in the even-aged secondary forests in Estonia (Lõhmus and Kraut 2010). Only *F. excelsior* formed a distinct snag stock in the cutovers (because of an extensive dieback due to a fungal pathogen; Bakys et al. 2009) but those snags remained standing for only a few years. Thus, it remains a challenge to include all tree species as snags in regenerating cutovers. Creating high stumps in final felling is a well-known option for spruce (Gustafsson et al. 2010), but in noble hardwoods, the benefits of artificial killing of trees over the retention of live individuals are not obvious, particularly when only small second-story trees are available. Possibly, the biota of all these shade-tolerant tree species can be better sustained in partial cutting systems, which are insufficiently studied from the biodiversity perspective in the European boreal and hemiboreal forests (but see Sippola et al. 2001; Lilja et al. 2005; Lõhmus et al. 2012).

The relative contribution of live-tree retention to the pool of downed CWD was small in the first post-harvest decade. Yet, the 5 m^3 ha^{-1} added are comparable to the typical amounts of all downed CWD in intensively managed Fennoscandian forests (Siitonen 2001), while the Estonian cutovers additionally had many sawn logs left on the sites. We do not know whether such logs host similar species assemblages as fallen retention trees, which can be very species rich (Junninen et al. 2007). However, compared with the situation in forests (Lõhmus and Kraut 2010), final felling increased the ground contact of downed CWD by two to four times, and that increase also continued later (Table 3). A major consequence of ground contact is the acceleration of decay (Mattson et al. 1987; Wei et al. 1997; Næsset 1999), which may already be unnaturally rapid in managed forests because of the properties of fast-grown wood (Edman et al. 2006). Thus, sawn logs probably decompose rapidly in clearcuts (see also Mattson et al. 1987, Janisch et al. 2005), and they also lack the dry and competition-free microhabitats typical of elevated downed wood (Dynesius et al. 2010). We suspect that microhabitat similarity of sawn logs and fallen retention trees is restricted to a few post-harvest years, and the contribution of retention trees will soon become distinct.

Conclusions and perspectives

Our results confirm that the habitat quality of clearcuts for wood-inhabiting biota critically depends both on the retention and on the post-harvest management of biological legacies (e.g. Lindenmayer and Franklin 2002). While semi-natural forests provide distinct opportunities for that, major improvements may still be needed. In Estonia, such improvements include more careful retention of snags in final felling; selecting larger retention trees; if carried out, then focusing slash harvest on the fine debris of common tree species; and providing snags of late-successional tree species.

Because CWD pool is expectably at its minimum in young or mid-aged forests (Siitonen 2001), additional problems may be discovered when expanding the time frame of studies. We did not observe a clear loss of forest type-specific features in final felling: similarly to pre-harvest forests (Lõhmus and Kraut 2010), cutovers retained, for example, fewer DW in dry forests, and the absolute and relative diversity of tree species and decay stages. However, the following dynamics suggested that homogenisation may become pronounced later on. A specific problem may be related to bark microhabitats, since bark loss and fragmentation (rather than wood decay; see also Mattson et al. 1987) were probably the main cause of the substantial loss of DW volumes. Ekbom et al. (2006) report more rapid bark loss on CWD in open conditions than under forest shade, which eventually may cause habitat scarcity for bark-inhabiting fauna. However, because of the large variation among sites that decreased the power to detect DW dynamics, there is a need for repeated sampling, notably on slash harvest sites where the reduced and well-exposed DW may have distinct dynamics.

Our study highlighted the following issues for which we currently lack scientific insight: (1) the consequences on biodiversity of the high turnover of downed CWD items, which tends to be concealed by much smaller changes in site-scale volumes (Gibb et al. 2005; Eräjää et al. 2010; this study). Theoretically, such turnover might negatively affect dispersal-limited organisms, but the wood-continuity

requirements of species are still poorly known (Jonsson et al. 2005); (2) the methods for spatially explicit planning of DW pools on the landscape scale. It is not obvious (and may be unachievable) that DW pool should meet a full array of biodiversity targets in every cutover. Moreover, as highlighted by the case of late-successional tree species, low-level retention cutting is not the only timber harvesting option that should be included in such assessments; (3) joint planning of tree retention for sustaining live-tree and dead-tree values, given that tree deaths support wood dwellers but may be the main threat for rare epiphytes (e.g. Lõhmus and Lõhmus 2010) and, in the case of patch retention, for forest interior species (Jönsson et al. 2007). It is unlikely that every retained tree can be individually assessed, but the conservation targets can still perhaps be varied depending on the characteristics of the pre-harvest stand.

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